

Do pre-dispersal insect seed predators contribute to maintaining tropical forest plant diversity?

Article

Accepted Version

Gripenberg, S. (2018) Do pre-dispersal insect seed predators contribute to maintaining tropical forest plant diversity? *Biotropica*, 50 (6). pp. 839-845. ISSN 1744-7429 doi: <https://doi.org/10.1111/btp.12602> Available at <https://centaur.reading.ac.uk/80229/>

It is advisable to refer to the publisher's version if you intend to cite from the work. See [Guidance on citing](#).

To link to this article DOI: <http://dx.doi.org/10.1111/btp.12602>

Publisher: Association for Tropical Biology and Conservation

All outputs in CentAUR are protected by Intellectual Property Rights law, including copyright law. Copyright and IPR is retained by the creators or other copyright holders. Terms and conditions for use of this material are defined in the [End User Agreement](#).

www.reading.ac.uk/centaur

CentAUR

Central Archive at the University of Reading

Reading's research outputs online

1
2 LRH: Gripenberg

3
4 RRH: Pre-dispersal Seed Predation by Insects

5
6
7
8
9 **Do pre-dispersal insect seed predators contribute to maintaining tropical forest plant**
10 **diversity?**

11
12
13 Sofia Gripenberg

14
15 Department of Zoology

16 OX1 3PS

17 University of Oxford

18 Oxford

19 UK

20
21 E-mail: sofia.gripenberg@zoo.ox.ac.uk

22
23
24 Received____; revision accepted____. (*Biotropica* will fill in the dates.)

25 **Abstract**

26 No abstract provided as manuscript is intended as a Commentary

27

28

29 **Key words:** density-dependence; fruit abscission; host specificity; Janzen-Connell hypothesis;

30 plant reproduction; seed predation

UNDERSTANDING THE MECHANISMS BEHIND THE EXTRAORDINARY LEVELS OF PLANT DIVERSITY
observed in many tropical forests is a key aim in tropical ecology (*e.g.*, Wright 2002, Leigh *et al.* 2004). What allows hundreds of tree species (Valencia *et al.* 1994) and a substantial number of liana species (Schnitzer *et al.* 2012) to co-occur locally in these forests? Among the many and mutually non-exclusive mechanisms proposed (Wright 2002), the role of natural enemies has received particular attention.

According to the Janzen-Connell hypothesis (Janzen 1970, Connell 1971), the coexistence – and the consequent high alpha diversity – of plant species in tropical forests is promoted by specialised natural enemies such as pathogens and insect herbivores that cause density- and/or distance-dependent patterns of plant survival. By making individuals more prone to enemy-attack when surrounded by conspecifics, plants will tend to fare better when conspecific density in the neighbourhood is low, thereby enhancing diversity at the community level. Many studies have documented distance- and density-dependence in the survival of seeds and seedlings in line with these predictions (for a recent meta-analysis, see Comita *et al.* 2014). Although it is often not clear what types of enemies contribute to observed patterns of plant mortality, data have slowly started to accumulate (*e.g.*, Bell *et al.* 2006, Mangan *et al.* 2010, Bagchi *et al.* 2014, Fricke *et al.* 2014).

The current literature on the role of enemies in plant diversity maintenance is dominated by studies assessing conspecific density and distance effects at relatively small spatial scales and focusing on seedlings or seeds that have already dispersed from the mother plant (*e.g.*, Harms *et al.* 2000, Bagchi *et al.* 2014). However, as noted by Gillett (1962), enemy-inflicted plant mortality with implications for diversity can also involve pests attacking seeds that are still attached to the mother plant. This idea was reiterated by Janzen (1970), who suggested that host-

specific pre-dispersal enemies can enhance diversity if they destroy a particularly large proportion of the seed crop where multiple reproductive conspecifics grow close to each other. However, in an alternative line of reasoning (see Fig. 2 and 3 in Janzen's publication), Janzen also illustrates how pre-dispersal enemies – regardless of their specificity – may in fact have the potential to *erode* plant diversity. According to this argument, the reduction in seed crop sizes caused by pre-dispersal enemies will truncate seed dispersal kernels, since with fewer seeds the probability of long-distance dispersal will decrease. This will inevitably decrease the distance between conspecific adults unless offset by foraging patterns of post-dispersal enemies and/or negative density-dependence acting across larger spatial scales. Almost 50 years on, while some aspects of Janzen's predictions have been hugely influential on empirical research, the pre-dispersal element has been largely neglected. As I argue below, pre-dispersal insect seed predators fulfil several criteria for being important diversity-enhancing plant enemies; yet they have been summarily ignored by ecologists interested in Janzen-Connell effects. Here I propose a research agenda for rectifying this.

CURRENT EVIDENCE. – Pre-dispersal insect seed predators have the potential to influence the ecological and evolutionary dynamics of their hosts (Kolb *et al.* 2007). Several lines of evidence suggest that they may also be important for plant diversity maintenance in tropical forests:

A large proportion of plant species are attacked by pre-dispersal seed predators and the number of seeds killed can be substantial. – Since Janzen's pioneering work on bruchid beetles in Costa Rica (1980), several studies have assessed patterns of insect seed predation in tropical forest plant communities in different parts of the world (Table 1). The results from these studies suggest that insect seed predation is common: a substantial proportion of surveyed plant species

were observed to be attacked by at least one species of insect seed predator, many of which are likely to have attacked the seeds while they were still attached to the mother plant. Only some of the studies in Table 1 attempted to quantify the proportion of seeds falling victim to predators through seed dissection or experimental manipulations. Where assessed, seed predation rates varied widely among species. While some authors (*e.g.*, Ctvrtecka *et al.* 2014) have concluded that their focal seed predator taxa are too rare to contribute to plant diversity maintenance, care should be taken in extrapolating such conclusions to other contexts and systems. It is worth noting that seed predation rates obtained through rearing or visual examination of seeds could severely underestimate the true impact of insect seed predators (Andersen 1988), for example where seed predators do not leave any clear feeding marks on their hosts. True seed predation rates are therefore likely to be higher than those reported in the literature.

Seed predators show remarkable levels of host-specificity. – For the Janzen-Connell mechanism to contribute to diversity maintenance, enemies need to be relatively specialised (Sedio & Ostling 2013, Stump & Chesson 2015). Several studies have assessed host specificity of internally feeding insect seed predators (*e.g.*, Janzen 1980, Ctvrtecka *et al.* 2014). An overall pattern to emerge is that these insects typically feed on one or a few closely related species and tend to be more specialised than other feeding guilds (Novotny *et al.* 2010; but see Sam *et al.* 2017). Less is known about the specificity of other guilds of seed-eating insects (*e.g.* sap-suckers and external feeders), but there is no doubt that at least the internally feeding seed predators are good candidate enemies in the context of plant diversity maintenance.

There is high potential for landscape-level density-dependence in pre-dispersal seed predation rates. – Studies testing for density-dependence of insect seed predation and/or seed survival over large spatial scales remain scarce (but see *e.g.* Visser *et al.* 2011). In one of the few

studies involving pre-dispersal seed predators, Jones and Comita (2011) assessed premature fruit abscission caused by a hymenopteran seed predator on *Jacaranda copaia* in the 50-ha forest dynamics plot on Barro Colorado Island (Panama). In line with Janzen's predictions, seed predation rates increased with increasing fruit densities. Nevertheless, this increase was not large enough to cancel out the positively density-dependent fruit set (a likely result of pollination success being highest in parts of the forest where there are many fruiting conspecifics). It is plausible that landscape-level density dependence in seed predation rates might occur in other species as well: The patchy distribution of host plants across the forest landscape (Condit *et al.* 2000) may impose spatial structure in insect abundances through behavioural responses of insects to local resource abundances. Studies of host-specific folivorous insect herbivores associated with trees in temperate regions have shown that the degree of host tree isolation can be an important determinant of landscape-level patterns of insect distribution (*e.g.*, Gripenberg *et al.* 2008, Tack *et al.* 2010). Spatially-structured populations driven by – and in turn potentially influencing – tree distributions may be particularly prevalent in species-rich tropical forests, since the low abundance of individual tree species will make their distributions patchy. Since the area as well as the isolation of habitat patches is key to influencing incidence and abundance in spatially-structured populations (*e.g.* Hanski 1994), it seems possible that any positive effects of landscape-level tree densities on seed predator incidence, abundance, and attack rates may be particularly pronounced in relatively small-sized tree species, where the small size of host individuals could lead to higher patch-level extinction rates.

WHAT NEXT? – Pre-dispersal seed predators cannot be dismissed as potentially important agents of diversity maintenance, but we are still a long way from answering the question of whether

they do indeed facilitate coexistence of plant species in tropical forests. The logistical challenges of studying seed predation in the canopy are substantial and community-level manipulations of pre-dispersal enemies analogous to those that have been done for post-dispersal enemies (Bagchi *et al.* 2014) will be unfeasible. To answer the question of whether pre-dispersal insect seed predators promote the coexistence of plant species in tropical forests a combination of multiple approaches (experiments, field observations, modelling) will therefore be needed. Below I identify a few starting points for moving the research field forward:

First, manipulative experiments excluding seed predators from selected plant individuals could yield important insights into the ecological role of pre-dispersal insect seed predators in tropical forests. These experiments could focus on single plant species, although it would be helpful to conduct experiments across a range of species to assess the generality of patterns observed. In addition to allowing us to quantify levels of seed predation, manipulative experiments could verify that pre-dispersal insect seed predators are indeed causing additional seed mortality: If, as has been suggested (Ghazoul & Satake 2009), trees sometimes initiate more seeds than could possibly be brought to maturity and then selectively abort insect-infested seeds, seemingly high levels of seed infestation rates recorded in observational studies may have little effect on plant fitness. In the context of plant diversity maintenance, it would be particularly interesting to assess the effects of seed predator exclusion on seed dispersal kernels and seedling recruitment curves (see Fig. 2 and 3 in Janzen, 1970), and to use sensitivity analyses to determine what levels of pre-dispersal seed predation would influence diversity through alternations in dispersal kernels. While experiments on single species do not answer the question of what happens in the wider community following seed predator exclusion, the community-level implications could be assessed by inputting results of individual species experiments to

models that predict community patterns (e.g. changes in species abundance distributions through early ontogeny) and exploring how community-wide patterns deviate from the predictions based on these models. Conducting manipulative experiments at the whole-tree scale does not come without challenges, but excluding pre-dispersal seed predators from selected tree individuals using insecticides (Louda 1982) or bagging (Nakagawa *et al.* 2005) – combined with appropriate control procedures – might be feasible for selected understorey tree species, for species producing seeds in discrete clusters (e.g. palms), or for species that can be accessed through one of the canopy cranes available for canopy research (e.g. Parker *et al.* 1992).

Second, further observational studies assessing spatial and temporal patterns of pre-dispersal seed predation are needed before generalisations about ‘typical’ responses of seed predators to variations in resource abundances can be made. A primary aim of these studies would be to test if the positive landscape-level density-dependence in seed predation hypothesised by Janzen (which could serve as a stabilising factor promoting species coexistence) occurs, or if seed predators are more typically satiated under high seed abundances. Given the potential scale-dependence of density-effects (Schupp 1992, Xiao *et al.* 2017), sampling protocols should be designed to allow testing for density-responses across multiple spatial scales. Since temporal variation in seed predation rates may also have implications for coexistence (Chesson 1985), studies should ideally be conducted over several fruiting seasons. The seed and fruit monitoring schemes established at some permanent forest dynamics plots (e.g. Anderson-Teixeira *et al.* 2015) could provide opportunities for assessing long-term temporal variation in seed predation rates if combined with protocols for scoring insect damage. Ideally, observational studies on density-responses of seed predators would be followed by modelling studies to assess whether observed density responses (which may be positive at some spatial scales, negative at other) are

sufficient to act as a mechanism regulating plant population growth. One challenge is that studies need to be conducted over large spatial scales given the potentially high dispersal ability of insect seed predators. For many species, existing forest dynamics plots may be too small for this purpose. Newly developed remote sensing techniques might prove useful when identifying landscape-level variation in conspecific densities of canopy trees over larger areas (see Jansen *et al.* 2008). Another challenge in quantifying pre-dispersal seed predation rates through observations is removal of seeds from the canopy by dispersers. Obtaining accurate estimates might still be feasible for species with cupules or other structures that are not removed by seed dispersers.

Third, although the focus of this commentary is on pre-dispersal seed predation, it is important to remember that plant performance with potential implications for coexistence is likely to be the result of multiple processes. We know little about the role of other taxa influencing pre-dispersal seed mortality, and even less about the ways in which they potentially enhance or hinder the influence of each other. There is room for both field-based and theoretical work assessing the combined effects of processes such as pollination, seed dispersal, and mortality caused by various groups of pre- and post-dispersal enemies on plant diversity, as well as studies integrating mortality processes at different stages of the plant life cycle (Green & Harms 2018). For example, it is known that feeding by insects in the canopy can affect the vigour of seedlings, and therefore the plant's tolerance to hazards at later stages (Sousa *et al.* 2003, Bonal *et al.* 2007). If we focus our efforts too narrowly on one enemy group and/or one specific life stage – as is often the case in work done to date – there is a risk that we miss or greatly underappreciate crucially important interactions.

CONCLUSIONS – There is ample scope for interesting work on the diversity-enhancing effects of pre-dispersal enemies paralleling work that has been done on post-dispersal enemies. This work would not only be of academic interest but also of potential importance in the context of current environmental changes. With fruiting patterns possibly changing following climate change (see *e.g.* Wright & Calderon 2006), this could lead to disruptions in the pre-dispersal seed predation process. Unless we know the ecological role of this enemy group, we don't know what the consequences are going to be for the diversity of plants in tropical forests.

ACKNOWLEDGMENTS

I thank Joe Wright, Owen Lewis and Yves Basset for helpful discussions and for comments on an earlier draft on this text. Feedback by Andy Jones, Noelle Beckman, Robert Bagchi and an anonymous reviewer helped improve the text. Some of the ideas presented in this essay were developed during field work on Barro Colorado Island funded by the Academy of Finland (project number 138299), the Royal Society (University Research Fellowship and RG130393), and GACR (16-20825S).

LITERATURE CITED

- ANDERSEN, A. N. 1988. Insect seed predators may cause far greater losses than they appear to. *Oikos* 52: 337-340.
- ANDERSON-TEIXEIRA, K. J., S. J. DAVIES, A. C. BENNETT, E. B. GONZALEZ-AKRE, H. C. MULLER-LANDAU, S. JOSEPH WRIGHT, K. ABU SALIM, A. M. ALMEYDA ZAMBRANO, A. ALONSO, J. L. BALTZER, Y. BASSET, N. A. BOURG, E. N. BROADBENT, W. Y. BROCKELMAN, S. BUNYAVEJCHEWIN, D. F. R. P. BURSLEM, N. BUTT, M. CAO, D. CARDENAS, G. B.

215 CHUYONG, K. CLAY, S. CORDELL, H. S. DATTARAJA, X. DENG, M. DETTO, X. DU, A.
 216 DUQUE, D. L. ERIKSON, C. E. N. EWANGO, G. A. FISCHER, C. FLETCHER, R. B. FOSTER, C.
 217 P. GIARDINA, G. S. GILBERT, N. GUNATILLEKE, S. GUNATILLEKE, Z. HAO, W. W.
 218 HARGROVE, T. B. HART, B. C. H. HAU, F. HE, F. M. HOFFMAN, R. W. HOWE, S. P.
 219 HUBBELL, F. M. INMAN-NARAHARI, P. A. JANSEN, M. JIANG, D. J. JOHNSON, M. KANZAKI,
 220 A. R. KASSIM, D. KENFACK, S. KIBET, M. F. KINNAIRD, L. KORTE, K. KRAL, J. KUMAR, A.
 221 J. LARSON, Y. LI, X. LI, S. LIU, S. K. Y. LUM, J. A. LUTZ, K. MA, D. M. MADDALENA, J.-R.
 222 MAKANA, Y. MALHI, T. MARTHEWS, R. MAT SERUDIN, S. M. MCMAHON, W. J. MCSHEA,
 223 H. R. MEMIAGHE, X. MI, T. MIZUNO, M. MORECROFT, J. A. MYERS, V. NOVOTNY, A. A.
 224 DE OLIVEIRA, P. S. ONG, D. A. ORWIG, R. OSTERTAG, J. DEN OUDEN, G. G. PARKER, R. P.
 225 PHILLIPS, L. SACK, M. N. SAINGE, W. SANG, K. SRI-NGERNYUANG, R. SUKUMAR, I. F. SUN,
 226 W. SUNGPALEE, H. S. SURESH, S. TAN, S. C. THOMAS, D. W. THOMAS, J. THOMPSON, B. L.
 227 TURNER, M. URIARTE, R. VALENCIA, M. I. VALLEJO, A. VICENTINI, T. VRŠKA, X. WANG,
 228 X. WANG, G. WEIBLEN, A. WOLF, H. XU, S. YAP, AND J. ZIMMERMAN. 2015. CTFS-
 229 ForestGEO: a worldwide network monitoring forests in an era of global change. *Global*
 230 *Change Biology* 21: 528-549.
 231 BAGCHI, R., R. E. GALLERY, S. GRIPENBERG, S. J. GURR, L. NARAYAN, C. E. ADDIS, R. P.
 232 FRECKLETON, AND O. T. LEWIS. 2014. Pathogens and insect herbivores drive rainforest
 233 plant diversity and composition. *Nature* 506: 85-88.
 234 BASSET, Y., C. DAHL, R. CTVRTECKA, S. GRIPENBERG, O. T. LEWIS, S. T. SEGAR, H. BARRIOS, J.
 235 W. BROWN, S. BUNYAVEJCHEWIN, B. A. BUTCHER, A. I. COGNATO, S. DAVIES, O. KAMAN,
 236 P. KLIMES, M. KNIZEK, S. E. MILLER, G. E. MORSE, V. NOVOTNY, N.
 237 PONGPATTANANURAK, P. PRAMUAL, D. L. J. QUICKE, R. K. ROBBINS, W. SAKCHOOWONG,

238 M. SCHUTZE, E. J. VESTERINEN, WEN-ZHI WANG, YUN-YU WANG, G. WEIBLEN, AND S. J.
 239 WRIGHT. 2018. A cross-continental comparison of assemblages of seed- and fruit-feeding
 240 insects in tropical rain forests: Faunal composition and rates of attack. *J. Biogeogr.*, in
 241 press. <https://doi.org/10.1111/jbi.13211>

242 BECKMAN, N. G., AND H. C. MULLER-LANDAU. 2011. Linking fruit traits to variation in
 243 predispersal vertebrate seed predation, insect seed predation, and pathogen attack.
 244 *Ecology* 92: 2131-2140.

245 BELL, T., R. P. FRECKLETON, AND O. T. LEWIS. 2006. Plant pathogens drive density-dependent
 246 seedling mortality in a tropical tree. *Ecol. Lett.* 9: 569-574.

247 BONAL, R., A. MUNOZ, AND M. DIAZ. 2007. Satiation of predispersal seed predators: the
 248 importance of considering both plant and seed levels. *Evol. Ecol.* 21:367-380.

249 CHESSON, P. L. 1985. Coexistence of competitors in spatially and temporally varying
 250 environments: a look at the combined effects of different sorts of variability. *Theoretical*
 251 *Population Biology* 28: 263-287.

252 COMITA, L. S., S. A. QUEENBOROUGH, S. J. MURPHY, J. L. ECK, K. XU, M. KRISHNADAS, N.
 253 BECKMAN, AND Y. ZHU. 2014. Testing predictions of the Janzen–Connell hypothesis: a
 254 meta- analysis of experimental evidence for distance- and density- dependent seed and
 255 seedling survival. *J. Ecol.* 102: 845-856.

256 CONDIT, R., P. S. ASHTON, P. BAKER, S. BUNYAVEJCHEWIN, S. GUNATILLEKE, N. GUNATILLEKE,
 257 S. P. HUBBELL, R. B. FOSTER, A. ITOH, J. V. LAFRANKIE, H. S. LEE, E. LOSOS, N.
 258 MANOKARAN, R. SUKUMAR, AND T. YAMAKURA. 2000. Spatial patterns in the distribution
 259 of tropical tree species. *Science* 288: 1414-1418.

260 CONNELL, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some
 261 marine animals and in rain forest trees. *In* P. J. Den Boer and G. R. Gradwell (Ed.).
 262 Dynamics of populations, pp. 298-312. PUDOC, Wageningen.
 263 CTVRTECKA, R., K. SAM, E. BRUS, G. D. WEIBLEN, AND V. NOVOTNY. 2014. Frugivorous weevils
 264 are too rare to cause Janzen–Connell effects in New Guinea lowland rain forest. *J. Trop.*
 265 *Ecol.* 30: 521-535.
 266 FRICKE, E. C., J. J. TEWKSBURY, AND H. S. ROGERS. 2014. Multiple natural enemies cause
 267 distance-dependent mortality at the seed-to-seedling transition. *Ecol. Lett.* 17: 593-598.
 268 GHAZOUL, J., AND A. SATAKE. 2009. Nonviable seed set enhances plant fitness: the sacrificial
 269 sibling hypothesis. *Ecology* 90: 369-377.
 270 GREEN, P. T. AND K. E. HARMS. 2018. The causes of disproportionate non-random mortality
 271 among life-cycle stages. *Ecology* 99: 36-46.
 272 GREIG, N. 1993. Predispersal seed predation on five *Piper* species in tropical rainforest.
 273 *Oecologia* 93: 412-420.
 274 GRIPENBERG, S., O. OVASKAINEN, E. MORRIEN, AND T. ROSLIN. 2008. Spatial population
 275 structure of a specialist leaf-mining moth. *J. Anim. Ecol.* 77: 757-767.
 276 HANSKI, I. 1994. A practical model of metapopulation dynamics. *J. Anim. Ecol.* 63:151-162.
 277 HARMS, K. E., S. J. WRIGHT, O. CALDERON, A. HERNANDEZ, AND E. A. HERRE. 2000. Pervasive
 278 density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature*
 279 404: 493-495.

280 HOSAKA, T., T. YUMOTO, Y. CHEN, I. SUN, S. J. WRIGHT, AND MD. N. NOOR (2011). Abundance
 281 of insect seed predators and intensity of seed predation on *Shorea* (Dipterocarpaceae) in
 282 two consecutive masting events in Peninsular Malaysia. *J. Trop. Ecol.* 27: 651-655.

283 JANSEN, P. A., S. A. BOHLMAN, C. X. GARZON-LOPEZ, H. OLFF, H. C. MULLER-LANDAU, AND S. J.
 284 WRIGHT. 2008. Large-scale spatial variation in palm fruit abundance across a tropical
 285 moist forest estimated from high-resolution aerial photographs. *Ecography* 31: 33-42.

286 JANZEN, D. H. 1970. Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104:
 287 501-528.

288 JANZEN, D. H. 1980. Specificity of seed-attacking beetles in a Costa Rican deciduous forest. *J.*
 289 *Ecol.* 68: 929-952.

290 JONES, F. A., AND L. S. COMITA. 2010. Density-dependent pre-dispersal seed predation and fruit
 291 set in a tropical tree. *Oikos* 119: 1841-1847.

292 JEFFS, C. T., P. KENNEDY, P. GRIFFITH, S. GRIPENBERG, L. MARKESTEIJN, AND O. T. LEWIS. 2018.
 293 Seed predation by insects across a tropical forest precipitation gradient. In press, *Ecol.*
 294 *Ent.*

295 LEIGH JR, E. G., P. DAVIDAR, C. W. DICK, J.-P. PUYRAVAUD, J. TERBORGH, H. TER STEEGE, AND
 296 S. J. WRIGHT. 2004. Why do some tropical forests have so many species of trees?
 297 *Biotropica* 36: 447-473.

298 LOUDA, S. M. 1982. Limitation of the recruitment of the shrub *Haplopappus squarrosus*
 299 (Asteraceae) by flower- and seed-feeding insects. *J. Ecol.* 70: 43-53.

300 MANGAN, S. A., S. A. SCHNITZER, E. A. HERRE, K. M. MACK, M. C. VALENCIA, E. I. SANCHEZ,
 301 AND J. D. BEVER. 2010. Negative plant-soil feedback predicts tree-species relative
 302 abundance in a tropical forest. *Nature* 466: 752-755.

303 NAKAGAWA, M., T. ITIOKA, K. MOMOSE, T. YUMOTO, F. KOMAI, K. MORIMOTO, B. H. JORDAL,
 304 M. KATO, H. KALIANG, A. A. HAMID, T. INOUE, AND T. NAKASHIZUKA. 2003. Resource
 305 use of insect seed predators during general flowering and seeding events in a Bornean
 306 dipterocarp rain forest. *Bull. Ent. Res.* 93: 455-466.

307 NAKAGAWA, M., Y. TAKEUCHI, T. KENTA, AND T. NAKASHIZUKA. 2005. Predispersal seed
 308 predation by insects vs. vertebrates in six Dipterocarp species in Sarawak, Malaysia.
 309 *Biotropica* 37: 389-396.

310 NOVOTNY, V., S. E. MILLER, L. BAJE, S. BALAGAWI, Y. BASSET, L. CIZEK, K. J. CRAFT, F. DEM,
 311 R. A. I. DREW, J. HULCR, J. LEPS, O. T. LEWIS, R. POKON, A. J. A. STEWART, G. ALLAN
 312 SAMUELSON, AND G. D. WEIBLEN. 2010. Guild-specific patterns of species richness and
 313 host specialization in plant–herbivore food webs from a tropical forest. *J. Anim. Ecol.* 79:
 314 1193-1203.

315 PARKER, G. F., SMITH, A. P., AND HOGAN, K. P. 1992. Access to the upper forest canopy with a
 316 large tower crane. *BioScience* 42: 664-670.

317 RAMÍREZ, N., AND A. TRAVESET. 2010. Predispersal seed-predation by insects in the Venezuelan
 318 Central Plain: overall patterns and traits that influence its biology and taxonomic groups.
 319 *PPEES* 12:193-209.

320 ROBERTSON, A. I., R. GIDDINS, AND T. J. SMITH. 1990. Seed predation by insects in tropical
 321 mangrove forests: extent and effects on seed viability and the growth of seedlings.
 322 *Oecologia* 83: 213-219.

323 SAM, K., R. CTVRTECKA, S. E. MILLER, M. E. ROSATI, K. MOLEM, K. DAMAS, B. GEWA, AND V.
 324 NOVOTNY. 2017. Low host specificity and abundance of frugivorous lepidoptera in the
 325 lowland rain forests of Papua New Guinea. *PLoS ONE* 12: e0171843.

326 SCHNITZER, S. A., S. A. MANGAN, J. W. DALLING, C. A. BALDECK, S. P. HUBBELL, A. LEDO, H.
 327 MULLER-LANDAU, M. F. TOBIN, S. AGUILAR, AND D. BRASSFIELD. 2012. Liana
 328 abundance, diversity, and distribution on Barro Colorado Island, Panama. *PloS ONE* 7:
 329 e52114.
 330 SCHUPP, E. W. 1992. The Janzen-Connell model for tropical tree diversity: Population
 331 implications and the importance of spatial scale. *Am. Nat.* 140: 526-530.
 332 SEDIO, B. E., AND A. M. OSTLING. 2013. How specialised must natural enemies be to facilitate
 333 coexistence among plants? *Ecol. Lett.* 16: 995-1003.
 334 SOUSA, W. P., P. G. KENNEDY, AND B. J. MITCHELL. 2003. Propagule size and predispersal
 335 damage by insects affect establishment and early growth of mangrove seedlings.
 336 *Oecologia* 135: 564-575.
 337 STUMP, S. M. AND P. CHESSON. 2015. Distance-responsive predation is not necessary for the
 338 Janzen-Connell hypothesis. *Theor. Pop. Biol.* 106: 60-70.
 339 TACK, A. J. M., O. OVASKAINEN, P. PULKKINEN, AND T. ROSLIN. 2010. Spatial location dominates
 340 over host plant genotype in structuring an herbivore community. *Ecology* 91: 2660-2672.
 341 VALENCIA, R., H. BALSLEV, AND G. PAZ Y MIÑO C. 1994. High tree alpha-diversity in
 342 Amazonian Ecuador. *Biodivers. Conserv.* 3: 21-28.
 343 VISSER, M. D., H. C. MULLER-LANDAU, S. J. WRIGHT, G. RUTTEN, AND P. A. JANSEN. 2011. Tri-
 344 trophic interactions affect density dependence of seed fate in a tropical forest palm. *Ecol.*
 345 *Lett.* 14: 1093-1100.
 346 WESSELINGH, R. A., M. WITTEVELDT, J. MORISSETTE, AND H. C. M. DEN NIJS. 1999.
 347 Reproductive ecology of understory species in a tropical montane forest in Costa Rica.
 348 *Biotropica* 31: 637-645.

349 WRIGHT, J. S. 2002. Plant diversity in tropical forests: a review of mechanisms of species
350 coexistence. *Oecologia* 130: 1-14.

351 WRIGHT, S. J., AND O. CALDERÓN. 2006. Seasonal, El Niño and longer term changes in flower
352 and seed production in a moist tropical forest. *Ecol. Lett.* 9: 35-44.

353 XIAO, Z., X. MI, M. HOLYOAK, W. XIE, K. CAO, X. YANG, X. HUANG, AND C. J. KREBS. 2017.
354 Seed–predator satiation and Janzen–Connell effects vary with spatial scales for seed-
355 feeding insects. *Annals of Botany* 119: 109-116.

356 XU, Y., Z. SHEN, D. LI, AND Q. GUO. 2015. Pre-dispersal seed predation in a species-rich forest
357 community: Patterns and the interplay with determinants. *PLoS ONE* 10: e0143040.

358

359

TABLE 1. Summary of data sets on insect seed predation in tropical forest plant communities, as obtained from the literature. Studies were identified using literature searches (Web of Science and Google Scholar; search terms seed predat* AND insect* AND tropic*) and through reference lists of relevant publications. The Google Scholar search yielded a large number of studies. These were sorted according to relevance, and only the top 500 studies were assessed for suitability based on title and/or abstract. Case studies focussing on single plant species were excluded, since the selection of focal species is likely to be biased towards species with particularly high predation rates. In studies denoted with an asterisk (*), the focus was not exclusively on pre-dispersal enemies, although it seems likely (based on sampling methodology and taxa involved) that a substantial proportion of the seed predation will be inflicted by enemies attacking seeds prior to seed dispersal. In most cases, sampling is unlikely to be exhaustive, and more plant-seed predator interactions would likely have been detected had sample sizes been larger. Hence, the values of the number and % of attacked species reported are likely smaller than true values.

Source	Focal seed predator group	Geographical region	Method used to assess incidence and rates of seed predation	Type of seeds examined (mature or immature)	Number of plant species studied	Number (and %) of plant species attacked	Proportion of seeds attacked per plant species (min-max) ^a
*Basset <i>et al.</i> 2018	All internally feeding seed predators	Lowland rainforests of Panama (Barro Colorado Island)	Rearing of internally feeding insect seed predators	Freshly fallen mature and immature fruits and seeds collected mostly from the ground	497 ^b	319 (64.2%) ^b	Not reported
*Basset <i>et al.</i> 2018	All internally feeding seed predators	Southern Thailand (forests surrounding the 24-ha ForestGEO plot in Khao Chong)	Rearing of internally feeding insect seed predators	Freshly fallen mature and immature fruits and seeds collected mostly from the ground	357 ^b	255 (71.4%) ^b	Not reported

*Basset <i>et al.</i> 2018	All internally feeding seed predators	Lowland rainforests of Papua New Guinea (seed and fruit samples collected in and around the ForestGEO 50-ha forest dynamics plot in Wanang)	Rearing of internally feeding insect seed predators	Freshly fallen mature and immature fruits and seeds collected mostly from the ground	332 ^b	257 (77.4%) ^b	Not reported
Beckman & Muller-Landau 2011	All insect seed predators	Dry, semi- deciduous forest in Panama (Parque Metropolitano)	Insecticide application	Mature and immature	7	4 (57.1%)	0.03-0.11 ^c
*Ctvrtecka <i>et al.</i> 2014	Internally feeding Curculionidae	Lowland rainforests of Papua New Guinea (two sites in the Madang province)	Rearing of internally feeding insect seed predators	Mature or nearly mature fruits; pre- and post- dispersal	326 ^d	106 (32.5%)	Not reported ^e
Greig 1993	All insect seed predators (main taxa Hemiptera and Coleoptera); most seed predators likely to be external feeders	Lowland rainforests of Costa Rica (La Selva)	Experimental exclusion of insect seed predators; infrutescences monitored throughout development	Mature and immature	5	5 (100%)	0.09-0.87 ^f
Hosaka <i>et al.</i> 2011	All internally feeding seed predators	Dipterocarp forest, Pasoh forest reserve, Malaysia	Rearing of internally feeding insect seed predators; seed dissections	Not reported	3 ^g	3 (100%)	Fruiting season 1: 0.27-0.34 Fruiting season 2: 0.35-0.49

*Janzen 1980	Internally feeding beetles (primarily bruchids)	Lowland dry forests of Costa Rica	Rearing of internally feeding insect seed predators	Ripe or nearly ripe seeds and fruits; collected from parent plant or ground below it	~975	110 (~8.9%)	Not reported
*Jefferies <i>et al.</i> 2018	All internally feeding seed predators (Coleoptera, Lepidoptera, Diptera)	Lowland forests of Panama (8 sites)	Visual examination of dissected seed samples	Freshly fallen mature and immature fruits and seeds collected from the ground	34	15 (44%)	0.018-1 ^h
Nakagawa <i>et al.</i> 2003	Internally feeding seed predators (Lepidoptera, Coleoptera)	Tropical lowland forest in Lambir Hills, Malaysia	Rearing of internally feeding insect seed predators	Seeds collected from seed traps. Maturity stage not mentioned, but likely mature or close to maturity.	1996: 26	1996: 25 (96.2%)	1996: 0.007-0.143 ⁱ
					1998: 15	1998: 13 (86.7%)	1998: 0.002-0.492 ^j
Nakagawa <i>et al.</i> 2005	Internally feeding insect seed predators	Tropical lowland forest in Lambir Hills, Malaysia	Rearing of internally feeding seed predators + examination of dissected seeds	Freshly fallen immature and mature seeds and fruits collected from seed traps. ^k	6	6 (100%)	0.235-0.784 ^l
Ramirez & Traveset 2010	All internally feeding insect seed predators	Venezuelan Central Plain (not only forest habitats)	Rearing of internally feeding seed predators	Seeds ready or nearly ready for dispersal; samples taken directly from the parent plant	187	89 (47.6%)	Not reported
*Robertson <i>et al.</i> 1990	All seed-boring insects (Coleoptera, Lepidoptera, Diptera, Hymenoptera)	Mangrove forests at 12 sites in tropical Queensland, Australia	Propagules scored for signs of insect attack (holes, feeding tracks)	Mostly fallen propagules; for some tree species seeds also collected from the plant	12	12 (100%)	0.062-0.803 ^m
*Sam <i>et al.</i> 2017		Lowland rainforests of Papua New Guinea (two sites)	Rearing of internally feeding seed- and fruit-associated Lepidoptera	Mature or nearly mature fruits; pre- and post-dispersal	326 ^d	171 (52.5%)	Not reported ⁿ

		in the Madang province)					
Wesselingh <i>et al.</i> 1999	Internally feeding seed predators (Hymenoptera, weevils)	Two sites in tropical montane forest in Costa Rica (Cordillera de Talamanca)	Visual examination of seeds	Mature seeds	4	4 (100%)	0.082-0.560 ^a
Xu <i>et al.</i> 2015	All pre-dispersal seed predators (insects and vertebrates) leaving feeding marks on seeds.	Mixed evergreen-deciduous broadleaf forest in subtropical China (Dalaoling Nature Reserve, Hubei Province)	Visual examination of seed samples	Seeds at different stages of maturity collected from traps	44	17 (38.6%)	0.002-0.556 ^p

^aIncludes only the subset of plant species attacked by insect seed predators.

^bData obtained from lead author.

^cTable A1 in *Ecological Archives* E092-185-A1

^dConsidering only species with samples comprising min 50 fruits weighing min 1kg.

^eNot reported, but likely to be low. [“(…) one weevil per 33 individual fruits on average”]

^fSeed predation rates reported in Table 3.

^gSeven species included in study, but intensity of seed predation only recorded for three.

^hSeed predation rates reported in Table 2. *Inga* sp. excluded, and only one entry for *Oenocarpus mapora*.

ⁱApproximate seed predation rates inferred from data in Appendix 1, assuming that one insect individual typically emerges from each infested seed. Scolytidae excluded when estimating proportion of seeds attacked, since for this taxon multiple individuals often emerge from each infested seed (pers. obs.).

^jApproximate seed predation rates inferred from data in Appendix 2, assuming that one insect individual typically emerges from each infested seed. Scolytidae excluded when estimating proportion of seeds attacked, since for this taxon multiple individuals often emerge from each infested seed (pers. obs.).

^kPredation rates reported only for mature seeds (but acknowledged in the source article that immature fruits were also commonly attacked by insects).

^lSeed predation rates reported in Table 2.

^mSeed predation rates reported in Table 1. Species-specific means obtained by pooling data from different sites.

ⁿNot reported, but likely to be low [“(…) low incidence of seed damage”]

^oSeed predation rates reported in Table 6.

^pSeed predation rates reported in Table 1. Estimates include both insects and vertebrates, but insects were the dominant seed predator group (74.9% of seeds showed signs of damage by insects, 25.1% showed signs of damage by vertebrates)